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Fundamental Unpredictability in Multispecies Competition

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ABSTRACT: One of the central goals of ecology is to predict the distribution and abundance of organisms. Here, we show that, in ecosystems of high biodiversity, the outcome of multispecies competition can be fundamentally unpredictable. We consider a competition model widely applied in phytoplankton ecology and plant ecology in which multiple species compete for three resources. We show that this competition model may have several alternative outcomes, that the dynamics leading to these alternative outcomes may exhibit transient chaos, and that the basins of attraction of these alternative outcomes may have an intermingled fractal geometry. As a consequence of this fractal geometry, it is impossible to predict the winners of multispecies competition in advance.

Keywords: biodiversity, chaos, resource competition, fractal basin boundaries, phytoplankton, prediction.

More individuals are born than can possibly survive. A grain in the balance will determine which individual shall live and which shall die, which variety or species shall increase in number, and which shall decrease, or finally become extinct. (Darwin 1859, p. 467)

Darwin, as this famous quote testifies, was well aware that the outcome of competition may depend on tiny differences. Here, we show that Darwin's "grain in the balance" can have a fractal structure. This fine-grained fractal structure makes it impossible to predict the winners of multispecies competition.

We consider a resource competition model widely used in plankton ecology and plant ecology. Theory (León and

Tumpson 1975; Tilman 1982, 1988; Huisman and Weissing 1995; Grover 1997) and experiments (Tilman 1977, 1982; Sommer 1986; van Donk and Kilham 1990; Rothhaupt 1996; Huisman et al. 1999) based on this model reveal that competition for one or two resources leads to a stable and predictable species composition. Motivated by the early findings of Gilpin (1975), May and Leonard (1975), Smale (1976), and Armstrong and McGehee (1980), we recently discovered that competition for three or more resources may generate oscillations and chaotic fluctuations in species abundances (Huisman and Weissing 1999, 2000, 2001). Here, we show that the predictions of resource competition models can become even more complicated. For this purpose, we make a distinction between the "time course" of competition and the "outcome" of competition. Chaos implies that the time course of competition shows sensitive dependence on initial conditions. That is, the long-term dynamics of the species are unpredictable. However, in case of a single chaotic attractor, it is still possible to predict which of the species will persist and within which bounds these species will fluctuate. In this article, we demonstrate that multispecies competition can also become unpredictable in a more surprising sense: it may be impossible to predict the outcome of competition. It may be impossible to foretell which of the species will be excluded and which will remain.

Competition Model

We consider n species competing for three abiotic resources. Let N_i denote the abundance of species i , and let R_j denote the availability of resource j . The dynamics of the species depend on the availability of the resources. The dynamics of the resources depend on the rates of resource supply and the amounts of resources consumed by the organisms. The model reads (León and Tumpson 1975; Tilman 1977, 1982; Huisman and Weissing 1999)

$$\frac{dN_i}{dt} = N_i[\mu_i(R_1, R_2, R_3) - m_i],$$

$$i = 1, \dots, n, \quad (1a)$$

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$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^n c_{ji}\mu_i(R_1, R_2, R_3)N_i,$$

$$j = 1, \dots, 3. \quad (1b)$$

Here, $\mu_i(R_1, R_2, R_3)$ is the specific growth rate of species i as a function of the resource availabilities, m_i is the specific mortality rate of species i , D is the resource turnover rate, S_j is the supply of resource j , and c_{ji} is the content of resource j in species i . We assume that the specific growth rates follow a Monod equation (Monod 1950) and are determined by the resource that is most limiting, as in Von Liebig's (1840) "Law of the Minimum":

$$\mu_i(R_1, R_2, R_3) = \min\left(\frac{r_i R_1}{K_{1i} + R_1}, \frac{r_i R_2}{K_{2i} + R_2}, \frac{r_i R_3}{K_{3i} + R_3}\right), \quad (2)$$

where r_i is the maximum specific growth rate of species i , K_{ji} is the half-saturation constant for resource j of species i , and "min" is the minimum function. This model formulation is widely used and particularly suited for primary producers like phytoplankton (León and Tumpson 1975; Tilman 1977, 1982; Sommer 1986; van Donk and Kilham 1990; Rothhaupt 1996; Grover 1997; Huisman and Weissing 1999). The model also provides a conceptual framework for competitive interactions among terrestrial plants (Tilman 1982, 1988).

Chaos on Three Resources

Previous work based on this competition model revealed periodic oscillations on three resources and chaos on five resources (Huisman and Weissing 1999, 2001). Here, we start by noting that competition for three resources is actually sufficient to generate chaos (fig. 1). We consider five species. These five species form a complicated system that can best be described by two competing cycles. Species 1–3 form one cycle. Here, species 1 is a strong competitor for resource 3 but becomes limited by resource 1. Species 2 is a strong competitor for resource 1 but becomes limited by resource 2. Species 3 is a strong competitor for resource 2 but becomes limited by resource 3, and so on. This generates cyclic dynamics (Huisman and Weissing 1999, 2001). The second cycle has a similar structure but is now based on species 1, 4, and 5. The two cycles are connected via species 1, and the system switches chaotically back and forth between the two cycles. This structure is clearly visible in figure 1B. Simulations reveal that the time course of competition shows sensitive dependence on initial conditions, one of the characteristic features of chaos. But the outcome of com-

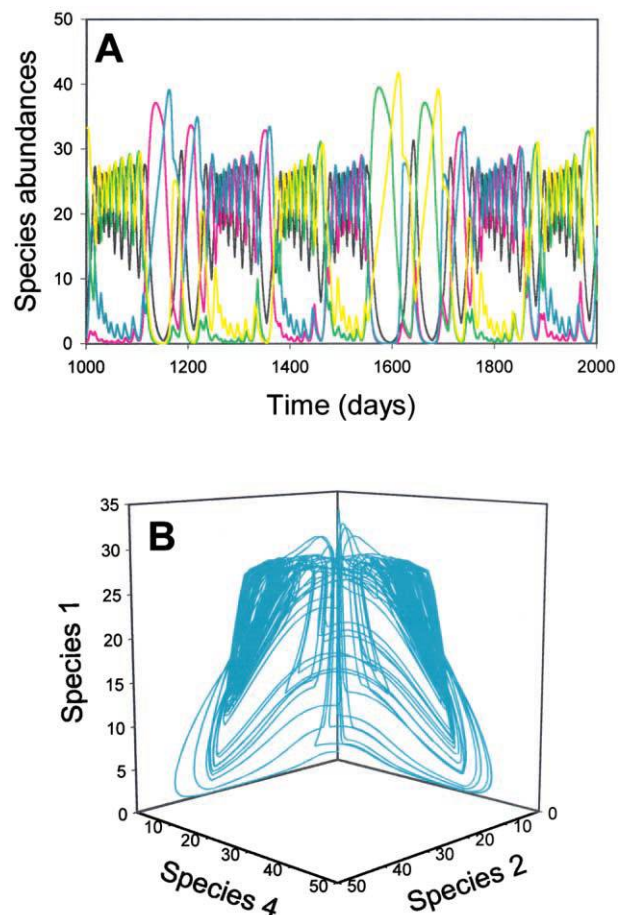


Figure 1: Chaos on three resources. *A*, Time course of competition. Black = species 1, red = species 2, blue = species 3, green = species 4, and yellow = species 5. *B*, The corresponding chaotic attractor. The attractor is plotted using three of the five species, for the period from $t = 1,000$ to $t = 4,000$ d. For parameter values, see appendix.

petition is independent of the initial conditions. Whatever the initial conditions, the system always ends up with the same five species on the same chaotic attractor (fig. 1B).

Fractal Basin Boundaries

For slightly different parameter combinations, the chaotic attractor of figure 1 breaks down and the two cycles become disconnected. Thus, now there are two attractors, two limit cycles to be precise. Simulations show that there is still a period of transient chaos during which the dynamics switch back and forth between the two limit cycles (fig. 2). The duration of this transient period is highly variable; it may last from <50 d to $>1,500$ d. In the end, the dynamics always

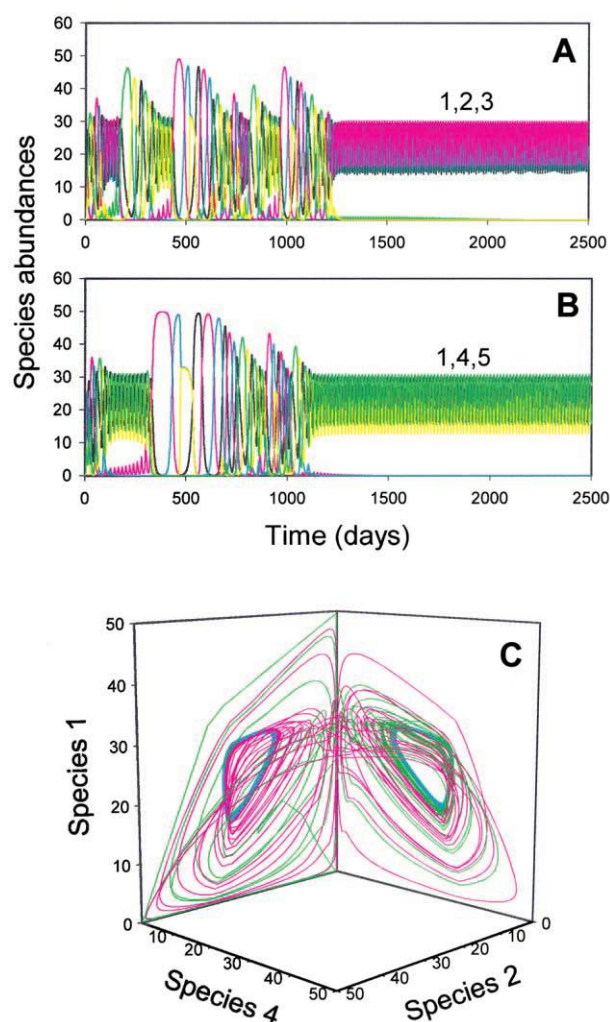


Figure 2: Transient chaos of five species competing for three resources. Depending on the initial conditions, the system settles at either (A) a limit cycle with species 1–3 as winners of competition or (B) a limit cycle with species 1, 4, and 5 as winners of competition. Black = species 1, red = species 2, blue = species 3, green = species 4, and yellow = species 5. C. The corresponding trajectories in phase space. The two limit cycles are indicated in blue. The red line is the trajectory corresponding to the time course in A, which finally settles at the limit cycle on the left-hand side. The green line is the trajectory corresponding to the time course in B, which finally settles at the limit cycle on the right-hand side. For parameter values, see appendix.

lead to one of the two limit cycles. If the system ends up at the limit cycle with species 1–3 (fig. 2A), the availability of resource 2 is too low for the persistence of species 4 and 5. If the system ends up at the limit cycle with species 1, 4, and 5 (fig. 2B), the availability of resource 3 is too low for the persistence of species 2 and 3. Which of the two

limit cycles is reached depends on the initial conditions (fig. 2C).

To investigate this system in detail, we plot the outcome of competition as a function of two parameters involved in the initial conditions: initial abundance of species 2 and initial abundance of species 4 (fig. 3). If species 1–3 win (as in fig. 2A), the outcome of competition is color-coded blue. If species 1, 4, and 5 win (as in fig. 2B), the outcome of competition is color-coded yellow. This yields a complicated pattern of speckles and stripes (fig. 3A). In the speckled areas, the outcome of competition is very sensitive to the initial conditions. If the speckled areas are magnified, new speckles and stripes appear (fig. 3B). Thus, the basins of attraction leading to the two alternative outcomes of competition appear to have fractal basin boundaries (*sensu* Grebogi et al. 1987).

The implication of this fractal geometry is that, within the speckled areas in figure 3, the predicted outcome of competition depends on the resolution at which the initial conditions are measured. Because initial conditions cannot be measured at infinite precision, it is impossible to predict with certainty what the outcome of competition will be.

Adding More Species

One might argue that limit cycles seem rare in ecosystems and that, hence, fractal basin boundaries are probably not something to worry about in the real world. There is an alternative possibility, however. Usually there are many species in an ecosystem, and some species may destroy the cyclic pattern. For example, consider a chaotic system of five species competing for three resources (fig. 4). At $t = 1,000$ d, we add three new species, labeled species 6, 7, and 8. These three species are potential winners. Species 6 is a strong competitor for resource 1; species 7, a strong competitor for resource 2; and species 8, a strong competitor for resource 3. It turns out that, within 100–200 d after invasion, one of the three added species becomes dominant (fig. 4A–4C). But which one? Again, we color-code the winner: yellow for species 6, red for species 7, and green for species 8. The winner appears to be extremely sensitive to the initial conditions (fig. 5). In fact, the fine-grained pattern in figure 5 is almost random. Thus, despite knowledge of all species traits and species interactions, it is impossible to predict in advance which of the species will become dominant. Only predictions in terms of probabilities make sense.

Discussion

We have shown that, for certain species combinations, competition for limiting resources generates fractal basin

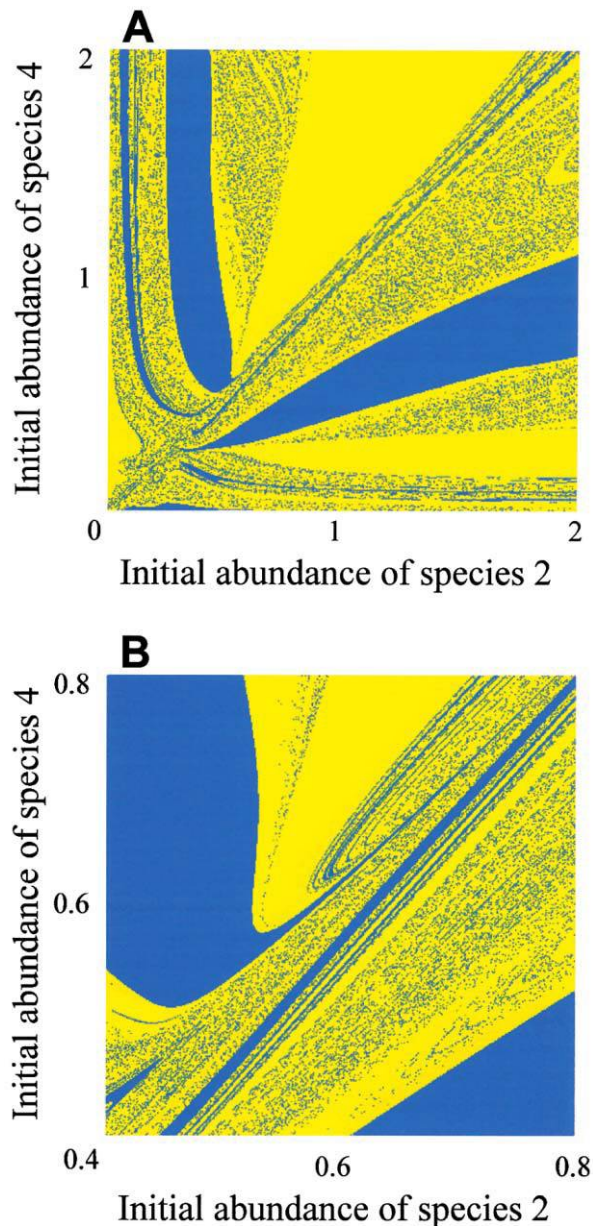


Figure 3: Fractal basin boundaries based on the five species of figure 2. The X-axis varies the initial abundance of species 2; the Y-axis varies the initial abundance of species 4. Pixels are colored blue if species 1–3 win. Pixels are colored yellow if species 1, 4, and 5 win. Part of A is magnified in B. In the speckled areas, the outcome of competition is very sensitive to the initial conditions. For parameter values, see appendix.

boundaries. Fractal basin boundaries are known for several dynamical systems (Moon and Li 1985; Grebogi et al. 1987; Sommerer and Ott 1993; Nusse and Yorke 1996; Neubert 1997). To the best of our knowledge, this is the first example of fractal basin boundaries in resource competition

models. The fractal geometry implies that the tiniest differences in initial conditions may lead to a different outcome of competition. Because it is impossible to measure infinitesimally small differences, it is impossible to predict the winners of multispecies competition with certainty.

We are still puzzled by the biological implications of these findings. First, in the real world, many factors have stochastic and unpredictable effects on the species composition of ecosystems. Few biologists would, therefore, argue against the suggestion that nature can be unpredictable. The unpredictability observed in this competition model, however, is at a much more fundamental level. Our results demonstrate that the winners of competition can be unpredictable in a fully deterministic setting without any stochastic ele-

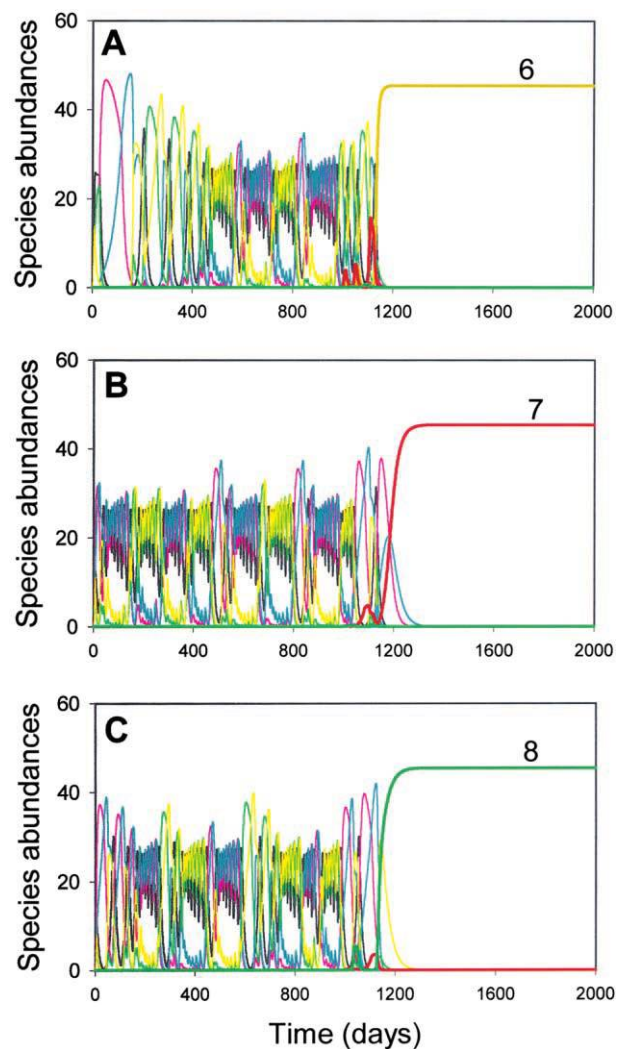


Figure 4: Transient chaos of eight species on three resources. Depending on the initial conditions either (A) species 6 wins, (B) species 7 wins, or (C) species 8 wins. For parameter values, see appendix.

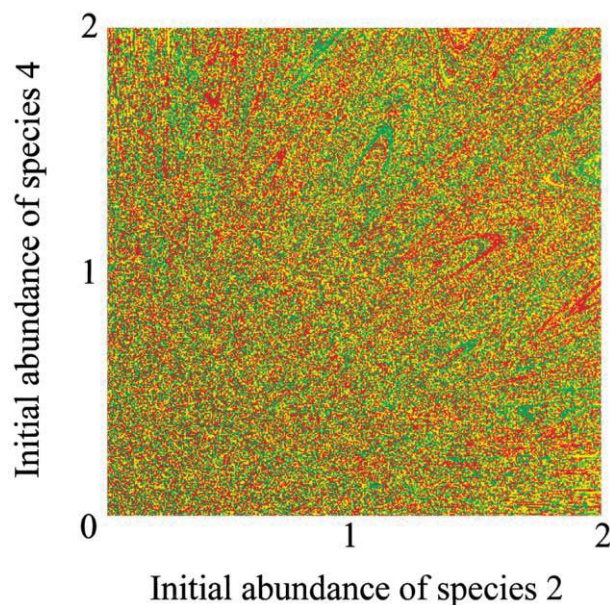


Figure 5: Fine-grained fractal basin boundaries based on the eight species of figure 4. The X-axis varies the initial abundance of species 2; the Y-axis varies the initial abundance of species 4. If species 6 wins, the pixel is colored yellow. If species 7 wins, the pixel is colored red. If species 8 wins, the pixel is colored green. The tiniest change in initial conditions can lead to a different winner of competition. For parameter values, see appendix.

ments. Second, whenever multispecies competition is unpredictable in a deterministic sense, the focus of research may shift toward probability calculus. Species with appropriate traits will still have a higher probability of dominating than species with inappropriate traits. Third, our results show that competition is unpredictable for certain species combinations. The results do not tell whether this unpredictability is a rare curiosity or a common phenomenon in the real world. Hence, our findings can best be interpreted as proof of principle or as a morality play that illustrates the potential complexity of multispecies interactions.

Nevertheless, it is worth emphasizing that we have used one of the standard competition models of ecology (Tilman 1982) with parameter values chosen within a realistic range for phytoplankton species. Based on extensive simulations (not shown), we conjecture that an essential ingredient for fractal basin boundaries in this model is the presence of multiple species or multiple sets of species that are each potentially strong enough to wipe out their competitors. We obtained fractal basin boundaries with a minimum constellation of five species and three resources (fig. 3). Preliminary simulations indicate that adding more species and more resources to this model greatly widens the potential

for fractal basin boundaries and associated unpredictable outcomes.

As a potential area of application, consider toxic phytoplankton. There are thousands of phytoplankton species. Most phytoplankton species are relatively harmless. A few species, however, are highly toxic, causing massive fish kills and a human health threat (Burkholder et al. 1992; Codd 1995; Anderson and Garrison 1997). Water managers try to forecast the occurrence of toxic phytoplankton species. Yet few predictive models appear successful (Anderson and Garrison 1997). One explanation for this predictive failure might be that phytoplankton assemblages consist of numerous species competing for a handful of resources, precisely the set of conditions used in this article. As the theory presented here suggests, under such circumstances, even with full knowledge of all species traits, it may be fundamentally impossible to forecast the dominance of toxic species.

In conclusion, our results show that multispecies competition is a very complicated process. For certain species combinations, Darwin's (1859) "grain in the balance" can have a fractal structure. As a consequence, the winners of multispecies competition can be as unpredictable as a throw of the dice.

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APPENDIX

Numerical Procedures and Parameter Values

Numerical simulations are based on a fourth-order Runge-Kutta procedure with a fixed time step of 0.01 d. The model is parametrized for phytoplankton. We use $r_i = 1 \text{ d}^{-1}$ and $m_i = D = 0.25 \text{ d}^{-1}$ for all species and $S_j = 10 \mu\text{mol L}^{-1}$ for all resources. These are typical values for phytoplankton grown in chemostats (Tilman 1977, 1982; Sommer 1986; van Donk and Kilham 1990; Rothhaupt 1996; Grover 1997; Huisman et al. 1999). Unless stated otherwise, initial conditions were $N_i(0) = 0.1$ for all species and $R_j(0) = S_j$ for all resources. Half-saturation con-

stants, K_{jp} , and resource contents, c_{jp} , are given in matrices **K** and **C** below. Different columns represent different species, and different rows represent different resources.

Figure 1 uses species 1–5 of figure 4. In figures 2 and 3,

$$\mathbf{K} = \begin{bmatrix} 0.20 & 0.05 & 1.00 & 0.05 & 1.20 \\ 0.25 & 0.10 & 0.05 & 1.00 & 0.40 \\ 0.15 & 0.95 & 0.35 & 0.10 & 0.05 \end{bmatrix},$$

$$\mathbf{C} = \begin{bmatrix} 0.20 & 0.10 & 0.10 & 0.10 & 0.10 \\ 0.10 & 0.20 & 0.10 & 0.10 & 0.20 \\ 0.10 & 0.10 & 0.20 & 0.20 & 0.10 \end{bmatrix}.$$

Initial conditions are default, except in figure 2A, $N_2(0) = 0.1$, and figure 2B, $N_2(0) = 0.2$.

In figures 4 and 5,

$$\mathbf{K} = \begin{bmatrix} 0.20 & 0.05 & 0.50 & 0.05 & 0.50 & 0.03 & 0.51 & 0.51 \\ 0.15 & 0.06 & 0.05 & 0.50 & 0.30 & 0.18 & 0.04 & 0.31 \\ 0.15 & 0.50 & 0.30 & 0.06 & 0.05 & 0.18 & 0.31 & 0.04 \end{bmatrix},$$

$$\mathbf{C} = \begin{bmatrix} 0.20 & 0.10 & 0.10 & 0.10 & 0.10 & 0.22 & 0.10 & 0.10 \\ 0.10 & 0.20 & 0.10 & 0.10 & 0.20 & 0.10 & 0.22 & 0.10 \\ 0.10 & 0.10 & 0.20 & 0.20 & 0.10 & 0.10 & 0.10 & 0.22 \end{bmatrix}.$$

Species 1–5 start at $t = 0$, each with default initial abundances, except figure 4A, $N_2(0) = 0.1$; figure 4B, $N_2(0) = 0.18$; and figure 4C, $N_2(0) = 0.3$. Species 6–8 invade at $t = 1,000$ d, each with an abundance $N_i(1,000) = 0.1$.

Figures 3 and 5 have a resolution of $400 \times 400 = 160,000$ simulations. The simulations were obtained by four personal computers running in parallel at a clock speed of 4×450 MHz for several days.

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